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Spatial displacement of Odonata in south-west Siberia

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A brief account is presented of mass dragonfly migrations observed previously in Russia and West Siberia in particular. A mass migration in *Libellula quadrimaculata* is described in detail. It occurred on 1 July 1981 in the south-western part of the West Siberian Plain in the valley of the Ishym River. From 1968 to 2008 we studied population dynamics, spatial distribution and displacement in dragonflies in the West Siberian forest-steppe. Detailed research was conducted at the biological station of the Russian Academy of Sciences near the Chany Lake. Mass migrations in *L. quadrimaculata* and some *Leucorrhinia* spp. followed situations with an extremely high population density and local mass aggregations and occurred with a period of *c*.10 years, correlated with fluctuation of water level in the region, mainly in the south. It is suggested that dragonfly migration not only optimizes their population size but increases the rate of transport of chemical elements and organic matter to dry land from eutrophic water bodies, which increases the importance of dragonflies to ecosystems at large.

Keywords: Odonata; dragonfly; spatial distribution; dispersal; migration; aggregation; population density; North Kazakhstan; Russia; West Siberia

Introduction

Extensive data on dragonfly migratory activity were presented by Corbet (1999). However, the phenomenon still raises many questions and seems to be an "eternal mystery" in odonatology.

Mass migrations are among the most intriguing phenomena in Odonata biology, and have always drawn attention of both professionals and the public. While reading up on the subject in the course of writing this article we found *c*.500 scientific publications containing data on dragonfly migrations. Most of them refer to densely populated Europe. A most informative survey was carried out by Dumont and Hinnekint (1973) on the problem of dragonfly migrations after large-scale dragonfly flights in West Europe in 1971; this was followed by the work of Gatter (1981) and others. The number of the corresponding publications dealing with Russia does not exceed 30; the number of those referring particularly to Siberia hardly amounts to 10. This fact can be explained by the relatively small number of professional researchers and amateurs interested in studying nature in Russia. As a consequence many amazing events pass by undetected and are

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not known to science. Thus, migrations probably occur in these areas as often as in Europe or any other large regions of the world.

Only a few Russian publications discuss detailed observations of dragonfly migrations and make attempts to explain them. One of the most interesting is a publication by Rodzyanko (1892), who described a migration of *Libellula quadrimaculata* Linnaeus in Poltavskaya province. As one of the reasons for its origin he identified the tendency of some dragonflies to form swarms and to blindly follow the flight of the first individual. A series of publications which are better known (Adelung, 1914; Averin, 1915; Bartenev, 1919; Kolosov, 1915; Sharleman, 1914) presented data on a mass migration of dragonflies in 1914, which covered the western part of the Russian Empire as well as West Siberia and Kazakhstan. Migrating swarms of *L. quadrimaculata*, sometimes mixed with small numbers of other species, could be seen throughout the whole huge territory from late April to the beginning of June. The directions were various. The authors accounted for those migrations mainly as the result of excessive emergence of one species and imitative behaviour impelling dragonflies to follow each other. The next report, and the only scientific report on a mass appearance of dragonflies in the neighbourhood of the town of Tobolsk in 1928, was published by Samko (1929). For the next 30 years data on dragonfly swarm appearance in West Siberia can be obtained in local mass media archives only; those data are few and only of historical interest. There are some publications in local newspapers describing dragonfly swarms flying through the towns of Kurgan and Tobolsk in 1922, Petropavlovsk and Omsk in 1930, and Omsk and Barabinsk in 1939. Judging by the descriptions the migrating species in all cases mentioned was *L. quadrimaculata.*

In the second half of the 20th century the problem drew attention to Belyshev (1958, 1963, 1973). In 1948 he witnessed and described in detail the initial stage of a mass flight of *L. quadrimaculata* in the upper reaches of the Ob River near the town of Biysk. The mass flight started on 14 June, at 05:00 h and continued till 15:00 h. Dragonfly swarms flew from north-east to south-west, i.e. from areas of the Ob valley, well supplied with water, in the direction of arid steppe in Kazakhstan. Taking into account his own observation and publications available, Belyshev suggested his concept of the origin of dragonfly migration. Its basic points are as follows: (1) migration is preceded by large population increases during several years of conditions favourable for larval development; (2) simultaneous mass emergence should be caused by a relatively long period of unfavourable weather conditions delaying metamorphosis and synchronizing adult emergence; (3) simultaneous take-off, a normal event during maiden flight, is determined by imitative behaviour; (4) the common flight direction is determined by the heliotaxis of immature dragonflies.

For reasons mentioned above, a comprehensive picture of dragonfly migrations in West Siberia proves to be unattainable. Having been studying dragonflies in Siberia for 40 years, however, we have collected substantial data, which could provide some contribution to the discussion of the still topical problem of migration in dragonflies. We witnessed mass flights in 1969 near Kurgan, in 1981 in North Kazakhstan, and in 1988, 1998 and 2003 near to the Chany Lake. We do not attempt a survey of the whole problem, which is impossible in the framework of one journal article, but will tackle the problem based mainly on our original data and sometimes making use of other sources.

Material and methods

Study area and study period

Some results of our dragonfly studies from 1968 to 2008 in south-west Siberia, namely in North Kazakhstan and part of the Russian territory – Omsk, Novosibirsk and Tomsk (partly) Provinces and the Altai region (partly) – are the basis of the article (Figure 1). Our research combined

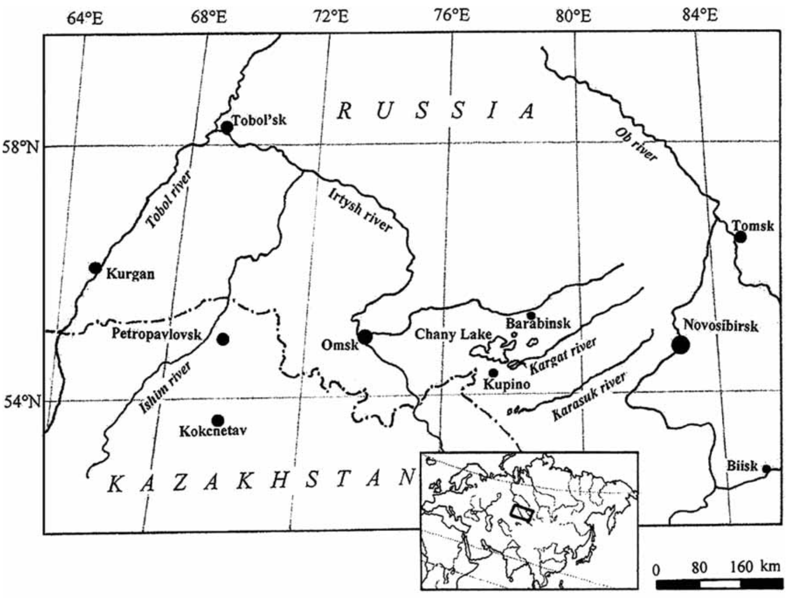

Figure 1. The territory of our research - south-west Siberia.

expeditions throughout the vast geographical region, with annual stationary work in the years 1972–2008 as a long-term monitoring project at the Chany biological station. This station was held by the Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences and was situated in the Baraba part of the West Siberian forest-steppe in the vicinity of the Chany Lake (54°37′ N, 78°13′ E) (Figure 1).

A mass dragonfly flight in North Kazakhstan in 1981 occurred in the zone of temperate arid steppe to the east of the Ishym River (52°58′ N, 66°39′ E). The landscape there was a flat plain sown with wheat.

Annual monitoring

The research techniques used were as follows: marking dragonflies, including a capture-recapture method; visual counting at belt transects; regular collecting of exuviae on selected sites; capture of adults in different habitats during timed 15-min intervals; sweep netting; and collecting larvae with a hydrobiological net. In addition some other supplementary techniques were used: counting aeshnid adults on routes by car; capturing libellulids with a net fixed on a car; counting the dynamic density of the population, i.e. counting the number of flights in a specified period of time over sites of a specified size in different habitats; floating traps for collecting winging adults; a special box trap on a drying water body bottom to collect larvae that had survived in water bodies that had dried up and/or frozen solid; and photo and video documentation. These methods allowed a detailed insight into the structure and dynamics of the dragonfly community at the site monitored, including interannual fluctuations in the number and spatial distribution of each species.

The data used to estimate anisopteran population densities were obtained mainly by two methods: visual timed flight counts on a belt transect and capture-mark-recapture studies. Belt transect counting was carried out near midday during the whole flight season at intervals of 2–10 days, or daily during peak seasonal activity of dragonflies. The transect length was *c*.350 m and the width 2 m, thus the area was 700 m^2. A person counting dragonflies moved at *c*.4 km per hour and

registered all dragonflies which took off or crossed the transect. The information was recorded on a portable dictaphone while counting. The number of anisopteran species flying simultaneously did not exceed seven, being usually three to four, and they could be easily identified at a distance by the skilled counters. The number of all dragonflies registered was divided by the area of the transect (700 m^2) to calculate density estimates of each species in three different habitats within the monitored site: (1) a herb meadow with thickets on the edge of a birch forest; (2) an abandoned field with field-protecting forest plantations; and (3) a steppe meadow adjacent to a lake. The numbers for each species were added up for periods of 10 days, a month and the whole season, maximum density was defined, and average density was estimated for each of these intervals.

To validate the data obtained on a transect for each of the most numerous species at its peak of abundance, a yearly registration using a capture-mark-recapture method was performed. Density (N) was estimated according to the formula $N = M \times n/m$, with $M =$ number of individuals marked, $n =$ number of individuals recaptured, $m =$ number of marked individuals among the recaptured ones. For example, 450 individuals of *L. quadrimaculata* were marked on the edge of a birch grove ($200 \times 50\,\text{m} = 1\,\text{ha}$) on 12 June 2003 from 08:00 h to 14:00 h. On the following day 450 individuals were caught again, five of them had been marked the day before. Thus, $N = 450 \times 450/5 = 40,500$ individuals. The density was obtained by dividing this figure by the area of the marking site (40,500 individuals in 10,000 m^2 = 4.05 individuals per m^2). On that very day of 13 June 2003, 1800 individuals of *L. quadrimaculata* were registered on a stretch 200 m long while moving along the transect crossing the site where we had marked. With a transect width of 2 m the density of *L. quadrimaculata* in that biotope was estimated at 4.5 specimens per m^2 (1800 individuals in 400 m^2). On 12–13 June 2004 the collecting area of the site on the edge of a birch grove was doubled to 2 ha. The density estimation on basis of mark-recapture came to 62,500 individuals or 3.1 individuals per m^2. Using the transect method, 3.5 individuals per m^2 were estimated. Thus the different methods resulted in well-correlated estimations; however the capture-mark-recapture method gave somewhat lower results.

Results

High population density followed high water level

The population size of *Libellula quadrimaculata* varied significantly during the monitoring period at the Chany biological station (Figure 2). In 1972 we counted a minimum of 0.04 individuals per m^2 and in 1988 a maximum of 10 individuals per m^2. Figure 2 shows that the annual population density correlated with the water level of the Chany Lake (correlation coefficient *c*.0.9) as a measure of the relative water supply of the whole region. One cycle of the level variation – from peak to peak – took eight years on average. The numbers of *L. quadrimaculata* reached the highest values in one or two years after a water level maximum. In periods of high water levels the number of water bodies increased and the living conditions in them improved, i.e. summer and winter oxygen deficiency decreased and the scale of drying up and freezing through decreased as well. Consequently, the number of suitable habitats increased and larval survival improved. The periods of low water supply level corresponded to low population density. The years of highest dragonfly population density were characterized by maximum migratory activity, in particular in 1988, 1998, 2003 and 2004.

Mass aggregations at Chany biological station

Long-term monitoring of the Libellulidae population state demonstrated that the distribution of *L. quadrimaculata* in different habitats was more uniform when the population density was low,

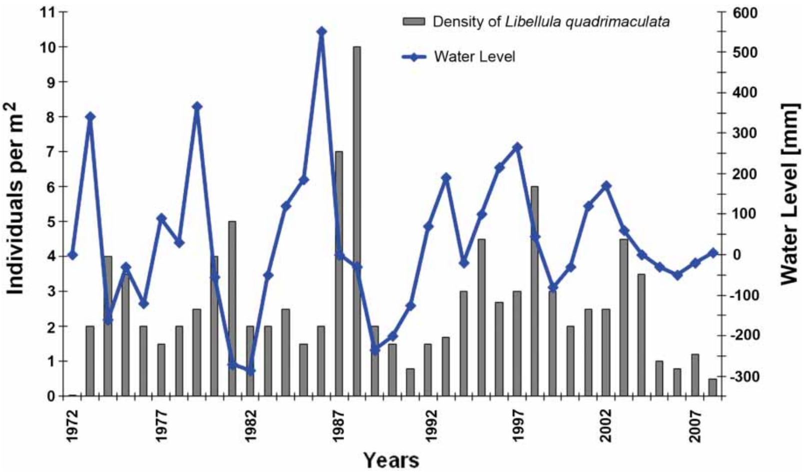

Figure 2. Long-term dynamics of water level fluctuations at the Chany Lake (line) and population density (mean seasonal value) of *Libellula quadrimaculata* (bars).

while a higher density led to their aggregation on the edge of a birch grove, sometimes resulting in local anomalous swarming of the insects. When the density in an aggregation exceeded three individuals per m^2, an exodus from the places of local concentration began. Such an exodus looked "unorganized", without gathering in a swarm. During the whole period of monitoring we observed from time to time dissipation of aggregations by an obvious flight of the dragonflies in southern and south-western directions, where they would gather with other local aggregations and form larger swarms. However, we never observed large dragonfly swarms in the northern part of the West Siberian forest-steppe, while in its southern part and in the steppe zone such swarms were recorded repeatedly. The most impressive formation of swarms was recorded by us in the steppe in northern Kazakhstan in 1981 (see below).

In early June 1988 many dragonflies aggregated along the edge of a birch grove with a length of 1800 m. In the daytime, when insects were most active, several thousand dragonflies could be seen in the air flying chaotically, the rustling of their wings creating an incessant noise background. Early in the morning grass, tree and shrub twigs were covered with dragonflies that were covered with dew. Counting dragonflies in the thickets showed that the density amounted to 210 individuals per m^2. In one wild-rose bush of *c*.1 m^3 480 *L. quadrimaculata* roosted. On the spots of dry nettle stems from the previous year the density of aggregation reached 500 individuals per m^2. In the open space apart from the forest the density was significantly lower.

To obtain a more accurate estimate of the density on a site as big as 50,000 m^2 within the whole standard study site, 500 *L. quadrimaculata* were marked in the morning of 6 June 1988. Recapture at the same place on the same day, with five marked individuals, allowed us to calculate the density to be 10 individuals per m^2. This result correlated with that obtained when counting with a big net fixed on a car riding fast through an aggregation of dragonflies along a specified route. Such dense aggregations occurred along a ribbon of birch forest along the delta of the Kargat River, the site occupying ca 40 ha, making it possible to estimate the aggregation at ca 4×10^6 individuals. Taking a mean individual live mass of 0.31 g into account, the whole mass must have been *c*.1240 kg.

From 8 June 1988 on, with sunny weather and a wind of *c*.5 m/s, the aggregation started declining fast, and no marked individual could be traced any more at the monitored site. The weather remained sunny with a south-west wind of 5–7 m/s. By mid-June the population density dropped to 0.7 individuals per m^2 due to displacement.

During the whole period we kept on visiting another birch grove 5 km north-west of the site monitored. There we observed another aggregation of *L. quadrimaculata* of similar density and size, which also started decreasing from 8–9 June on when individuals flew south- and south-westward. According to the evidence of numerous witnesses, the aggregations and displacements of dragonflies occurred in many places in the West Siberian forest-steppe in that time. For example, a "large dragonfly swarm resembling a dark cloud" was observed around midday on 18 June 1988 by residents of Kupino (pers. comm.), a town in arid steppe on the border of the Novosibirsk Province and Kazakhstan.

We also observed huge aggregations in other years, e.g. in 1998, 2003 and 2004 in the same habitats. The population density of *L. quadrimaulata* reached 6.0 individuals per m^2 by about 10 June 1998, 4.5 individuals per m^2 in 2003 and 3.5 individuals in 2004 (Figure 2). In all years with mass aggregations the high density fell abruptly as the dragonflies dispersed mainly southward. This mass exodus could be judged as the origin of migration.

In *L. quadrimaculata* aggregations, two *Leucorrhinia* species, *L. pectoralis* (Charpentier) and *L. rubicunda* (Linnaeus), were also present in different proportions. In some cases they made up only a small portion of the aggregation, while in others they made up half of the aggregation and sometimes even more. For instance, while marking Libellulidae on 2–3 June 2004 for a capture-recapture analysis, 600 *L. quadrimaculata* and 670 *Leucorrhinia* spp. were captured (25% *L. pectoralis* and 75% *L. rubicunda*). In this aggregation the sex ratio was unusual due to a majority of females: in *L. quadrimaculata* females made up 71%, in *L. pectoralis* 58% and in *L. rubicunda* 99%, while the sex ratio in other years was approximately equal. In mid-June that aggregation dispersed like all others and the dragonfly numbers decreased almost by a factor 20.

While *Leucorrhinia* and *Libellula* species exhibited aggregations and spatial displacements in the first half of the summer, similar phenomena were observed in *Aeshna* and *Sympetrum* species in the second half of the summer. *A. mixta* Latreille and *S. vulgatum* (Linnaeus) were involved in particular. Aggregation of *A. mixta* took place almost annually in the birch forest mentioned above. There were years when aggregation was inconspicuous, but sometimes it was striking. The largest aggregation of *A. mixta* in this habitat was observed in 2002, when the density from late August until early September amounted to 1.4 individuals per m^2. On 28–30 August 2002 738 *A. mixta* were captured for marking. Movements of *Aeshna* and *Sympetrum* as a rule seemed to be randomly oriented, though there were rare exceptions. For instance, in early August 1993 an intensive flight of *S. vulgatum* from north-west to south-east was observed. The insects flew in tandem formations 5 m above the ground, and though the distance between those pairs was not less than 10 m, the displacement basically looked like a migration stream. Similar movements of *S. vulgatum* pairs, as far as direction was concerned, were also observed in 1974, 1981, 1982, 1989 and 1999, but those were less intensive.

Mass flight in North Kazakhstan

On 1 July 1981 around midday at an ambient temperature of 23°C, variable cloud and SSW wind of *c*.5 m/s, a dark cloud became visible on the horizon in the north and was mistaken for a rainstorm cloud. The cloud approached rather fast and against the wind, and soon it became evident that it was a huge swarm of dragonflies. The front of the approaching mass was not less than 1 km wide, but to estimate its length was impossible. The lower boundary moved at 3–4 m above the ground, the thickness of the flying layer of the insects amounting to 20 m. At the very moment of passing the spot of observation the wind suddenly grew stronger and changed into a squall, with gusts of more than 25 m/s. Movements of the insects became chaotic and faster, the swarm abruptly flew lower, almost touching the ground, but gusty wind scattered the insects, and in a few minutes the swarm dispersed. The insects were partly blown away from the field of

vision, and many of them were forced into the wheat growing there. On the site of the catastrophe a granary building was situated with its front wall 15 m wide and 5 m high, standing in the way of the insects drawn by the wind. Many dragonflies were smashed on that wall, and it resulted in literal removal of a sector in the swarm that corresponded with the size of the wall. In a few minutes a rainstorm broke out. After the rainstorm a layer of dead and injured dragonflies was found beside the granary wall, the thickness being 0.2 m on average. Thus it was possible to count the number of dragonflies taken out from the swarm by the obstacle and to make a rough estimate of the number of the insects in the whole swarm. Around 7450 insects per m^2 were found on the ground beside the wall; 10 sites were counted with 1 m^2 each. The area covered by the insects was c.60 m^2, thus the obstacle 15 m wide removed c.447,000 insects from the swarm. The squall flattened the swarm, pressing it to the ground and its width did not decrease but rather widened, but it was difficult to give a more precise estimate. Taking the width of the swarm to be at least 1000 m, the 15 m sector containing c.0.5 million dragonflies would have corresponded to 1/66 part of it, so the number of the insects might have been c.30 million individuals. At the moment of the catastrophe a substantial portion of the dragonflies was carried by the wind over the obstacle, managed to avoid it or were injured but fell at a considerable distance from the wall where the calculation was done later, and many dead dragonflies from the top of the layer were carried away with the wind. Hence the figure is judged to be underestimated by at least 3–4-fold, and the true number of the dragonflies in the swarm must have approached 100 million individuals. A very rough estimate of the swarm mass gives c.30 tons, taking 0.31 g as an average mass of one insect.

Identification of the dragonflies recovered demonstrated that the swarm consisted of *Libellula quadrimaculata* (98%); *Leucorhinia pectoralis* (1.6%); *L. rubicunda* (0.38%); and *Cordulia aenea* (0.02%). Sex ratio was approximately equal. It is worth noting that most *L. quadrimaculata* individuals were mature and only 10% of them had juvenile pattern features. All *Cordulia* and *Leucorrhinia* individuals looked mature.

In the radius of 10s of kilometres from the place of the incident there are but a few water bodies suitable for dragonfly development. Of special interest is the direction of the flight – from north to south towards arid steppe and semi-deserts of Kazakhstan. During June of that year, numbers of dragonflies, and particularly of *L. quadrimaculata*, were recorded as high in the whole forest-steppe lying some 150 km to the north, an area rich in water bodies. By the end of June aggregations of this species were registered several times moving in different directions, and even clogging the automobile radiators at some parts of the roads. Aggregations of *L. quadrimaculata* were witnessed in other places in the southern part of West Siberia as well, particularly in the lower reaches of the Karasuk River and in the vicinity of the Chany Lake.

Long-term and interannual changes in relative abundance and species composition

Long-term monitoring of the dragonfly community in the vicinity of the Chany biological station revealed not only long-term but significant interannual fluctuations in the composition and numbers of species. A comparison of mean abundance data of three *Coenagrion* species, namely *C. armatum* (Charpentier), *C. lunulatum* (Charpentier) and *C. pulchellum* (Van der Linden), *Enallagma cyathigerum risi* Schmidt and *Erythromma najas* (Hansemann) in 1975–2006 is given in Figure 3. In all those years until 2005 there was no significant disparity in the population structure: the taxon assemblage and the ratio of their numbers were similar. But in 2006 a sharp change in the frequency ratio of the former three genera took place and two new species – *Coenagrion johanssoni* (Wallengren) and *Nehalennia speciosa* (Charpentier) suddenly appeared. Both species were met only twice during the 30 preceding years and each time only one individual was captured. In mid-July 2006 they were registered as common. By contrast, several other species appeared to be infrequent or even rare. Habitats within the Baraba forest-steppe appeared

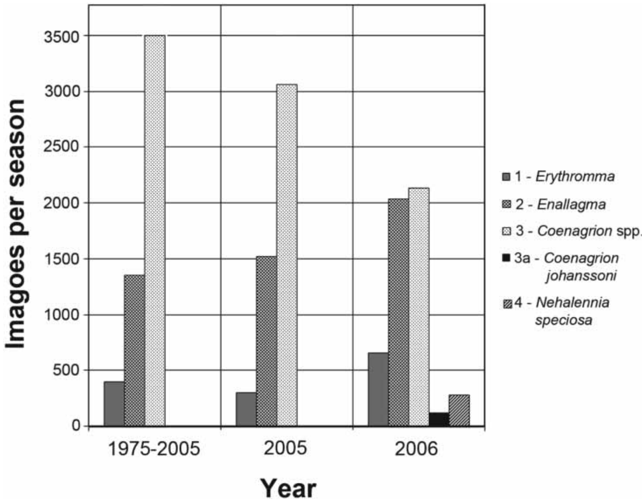

Figure 3. Interannual fluctuations in composition and abundance of some taxa of Coenagrionidae in the vicinity of the Chany Lake, south-west Siberia. Bars from the left: *Erythromma najas*; *Enallagma cyathigerum risi*; *Coenagrion* spp. (*C. armatum*, *C. lunulatum*, *C. pulchellum*); in 2006 only also *C. johanssoni*; *Nehalennia speciosa*.

to satisfy ecological requirements of such species as *Calopteryx splendens*, *Ischnura elegans*, *Anax parthenope*, *Epitheca bimaculata*, *Orthetrum cancellatum* and *Sympetrum pedemontanum* as well as *Platycnemis pennipes* (Pallas), *Gomphus* (*Stylurus*) *flavipes* (Charpentier) and *Ophiogomphus cecilia* (Fourcroy). Nevertheless, only single individuals of the first six species have been found in the region so far and the last three species have never been previously registered there, although one can find them in the east and west of that region within the boundaries of the West Siberian forest-steppe.

Conclusions

Our long-term observations of frequency and spatial displacement in dragonflies permitted of the following conclusions: (1) the structure of the regional fauna was subject to significant interannual fluctuations, with new non-characteristic species occurring occasionally, and sometimes becoming numerous; (2) some species tended to disperse far from their native water bodies after emergence; (3) strong fluctuation in population density, up to 100-fold, was typical of some species; (4) the tendency for massive spatial displacements grew with increasing density; (5) most flights observed showed a south-western, south-eastern or southern directions.

Discussion

According to our data from south-west Siberia and North Kazakhstan, we think sporadic mass migration – exodus flights of large numbers of individuals from a native habitat, resulting in the reduction of local excess population – takes place non-directionally, perhaps not aiming to find new habitat. The majority of migrants may die during any given event.

Such migrations are not common everywhere but may occur in abundant and widely distributed species inhabiting mostly lentic eutrophic water bodies. They are irregular but may correlate with climatic cycles, such as water level fluctuations; thus a tendency for approximately 10-year intervals between major migrations can be traced. Such relations are clearly seen in *Libellula*

quadrimaculata. Many individuals, in some cases the absolute majority of a local population, participate in the migration, while others stay in the native habitat, e.g. as larvae which have not yet finished metamorphosis. Some other local populations may join in the course of the migration.

Most publications dealing with dragonfly migration are devoted to mass migrations in this sense, discussing their stimuli and offering various explanations for their existence. Perhaps no universal explanation can be given, and migration events can follow various scenarios. One feature in common, however, is that participants in a sporadic mass migration, having perished accidentally, contribute to the intensification of nutrient cycling in ecosystems. At this point it is worth recalling the estimates of the biomass of a migrating swarm and the ecological fact that amphibious insects constitute the principal biogenic factor for returning many chemical elements from water bodies, situated in lower parts of landscapes, to dry land, normally situated in higher levels within the landscape, where they are driven by natural abiogenic drain (Belyshev, 1974; Haritonov & Popova, forthcoming).

The attempts to estimate the number of insects in migrating swarms are few and rough but always look very impressive. For instance, A. Fountaine, having witnessed a huge migration of dragonflies near the town of At in Belgium, estimated its number as “several hundred million dragonflies” (cited in Kornelius, 1866). Kornelius himself (1866) described the migration on 19 May 1862 in the vicinity of Mettmann in Germany and made a calculation that the swarm comprised 2,400,000,000 individuals. This figure might be overestimated, but in any case the scale of at least 100 million individuals is evidently valid. This fact is another evidence of the contribution which dragonflies may add to the functioning of ecosystems.

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